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Separate channels for processing form, texture and color:

Evidence from fMRI adaptation and visual object agnosia

Cavina-Pratesi C, Kentridge R W, Heywood C A, and Milner A D
Durham University, UK

Running title
Shape, Texture and Color processing

Correspondence to:

Dr C Cavina-Pratesi

Department of Psychology, Durham University

Science Laboratories, South Road

Durham DH1 3LE, UK

Phone +44-191-334-3258

Fax +44-191-334-3241

Email: cristiana.cavina-pratesi@durham.ac.uk

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Abstract (197 words, max is 200)

Previous neuroimaging research suggests that whereas object shape is analysed in the lateral occipital cortex, surface properties of objects, such as color and texture, are dealt with in more medial areas, close to the collateral sulcus (CoS). The present study sought to determine whether there is a single medial region concerned with surface properties in general, or whether instead there are multiple foci independently extracting different surface properties. We used stimuli varying in their shape, texture, or color, and tested healthy participants and two object-agnosic patients, in both a discrimination task and a functional MR adaptation paradigm. We found a double dissociation between medial and lateral occipito-temporal cortices in processing surface (texture or color) versus geometric (shape) properties, respectively. In Experiment 2 we found that the medial occipito-temporal cortex houses separate foci for color (within anterior CoS and lingual gyrus) and texture (caudally within posterior CoS). In addition we found that areas selective for shape, texture and color individually were quite distinct from those which respond to all of these features together (shape *and* texture *and* color). These latter areas appear to correspond to those associated with the perception of complex stimuli such as faces and places.

Key words: fMRA, visual agnosia, shape processing, color processing, texture processing.

Introduction

Although surface features such as texture and color allow the brain to infer the material of which an object is composed – a facility that is crucial for classifying objects in the natural world (Adelson EH, 2001), current research on the neural correlates of object recognition has focussed mainly on the role played by geometric features such as shape (Kourtzi Z and Kanwisher N, 2000; Murray SO et al., 2003), size (Cavina-Pratesi C et al., 2007; Murray SO et al., 2006) and orientation (Rice NJ et al., 2007; Valyear KF et al., 2006).

Surface cues can be highly diagnostic for object identification in natural versus manufactured objects (Biederman I and Ju G, 1988; Tanaka JW and Presnell LM, 1999), when recognition takes place among objects belonging to the same structural category (Price CJ and Humphreys GW, 1989), or when shape diagnosticity is reduced as a consequence of object occlusion (Tanaka JW and Presnell LM, 1999), poor vision (Wurm LH et al., 1993) or visual agnosia (Humphrey GK et al., 1994; Mapelli D and Behrmann M, 1997).

Brain areas associated with surface color (Hadjikhani N et al., 1998; Lueck CJ et al., 1989; McKeefry DJ and Zeki S, 1997), texture (Peuskens H et al., 2004) and pattern (Barrett NA et al., 2001) have been localized within the temporal-occipital region in people, yet their role in object recognition is still poorly understood. A major step forward has been taken by Goodale and co-workers (Cant JS et al., 2009; Cant JS and Goodale MA, 2007) who proposed the existence of a division of labor between lateral and medial occipital cortices for discriminating geometric versus material properties of objects, respectively. They showed that while geometric properties of meaningless objects activated the lateral occipital cortex (LOC), surface properties of the same objects activated more medial areas near the collateral sulcus

(CoS). In line with these results, we recently provided evidence that areas respectively activated by shape and texture play a causally necessary role in the perceptual discrimination of these features (Cavina-Pratesi C et al., 2009). We tested two patients with visual object agnosia, one of whom (DF: Milner AD et al., 1991) performed well on our texture discrimination task but at chance on the shape discrimination task, while the other (MS: Newcombe F and Ratcliff G, 1975) showed the converse pattern. We were able to match this behavioral double dissociation with a parallel neuroimaging dissociation, finding activation in medial occipito-temporal cortices only in patient DF during texture discrimination, and activation in lateral occipito-temporal cortex only in patient MS during shape discrimination.

The evidence thus suggests that medial occipito-temporal mechanisms are specialized for resolving the surface features that can signal the material of which an object is composed. It should be noted, however, that although Goodale and his co-workers varied the surface features of their stimuli in terms of texture and color, they failed to demonstrate the existence of independent brain modules for texture and color within the medial occipito-temporal cortex (Cant JS *et al.*, 2009).

The aim of the present study was threefold. First, we planned to investigate whether the medial occipito-temporal cortex processes surface properties in general (including both texture and color) or whether it houses separate foci that extract different surface features (texture versus color). Second, we planned to investigate whether separate information about geometric and surface features would converge in "higher" areas of the occipitotemporal cortex, which might combine shape, texture and color features as conjoint "objects". Third, we aimed to replicate our previous results on the necessary role played by lateral and medial occipito-temporal cortices in discriminating geometric and surface features, respectively, by using a novel set of

stimuli and a different experimental paradigm. We used images of virtual three-dimensional (3D) stimuli varying in their geometric (shape) or surface (texture or color) features and asked neurologically healthy participants, and two object-agnosic patients, to perform a behavioral discrimination task (Experiment 1), and a functional magnetic resonance adaptation (fMRA) task (Experiment 2). The two patients (MS and DF) suffer from visual agnosia as a consequence of selective lesions of their visual ventral streams. However, while patient DF's perceptual deficit focuses on the geometric features of objects, leaving her ability to extract texture and color spared (Humphrey GK *et al.*, 1994; Milner AD *et al.*, 1991), patient MS's perceptual deficit is centered on color (achromatopsia, Heywood CA and Kentridge RW, 2003) and texture (Cavina-Pratesi C *et al.*, 2009). Quite unlike DF, MS's perception of geometric structure (when the contours are clearly defined) remains intact (Kentridge RW et al., 2004).

Material and Methods

Images of virtual 3D objects resembling furry balls which could vary in shape or in the surface dimension of texture or color (Figure 1) were used with neurologically intact participants and two object-agnosic patients (MS and DF) both behaviorally (Experiment 1) and in the MRI scanner (Experiment 2).

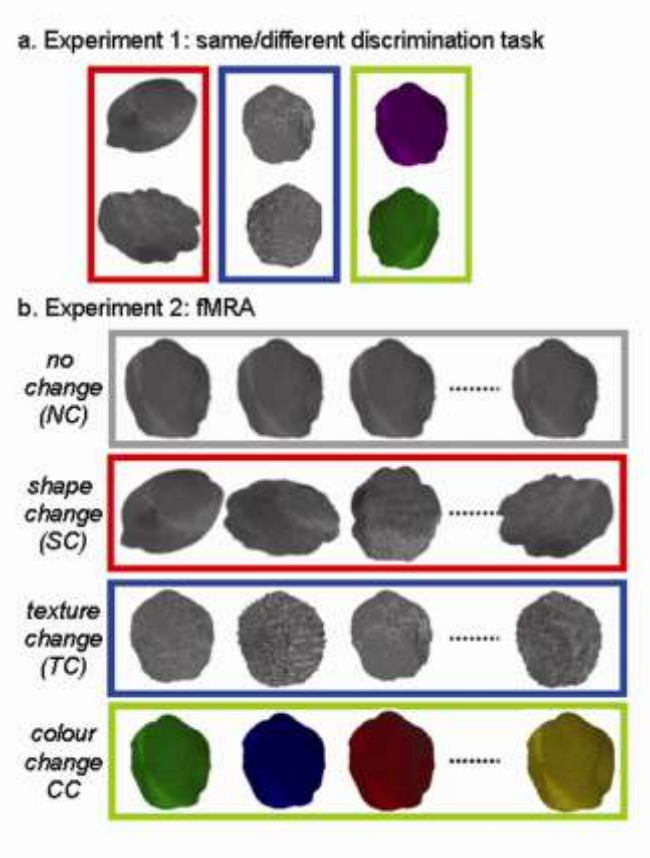

Figure 1. Visual stimuli for Experiments 1 and 2 were assembled using virtual three dimensional textured irregular objects resembling furry balls. a) In Experiment 1, participants were asked to perform same/different judgments on objects that could vary in shape, texture or color only. Examples of trials are shown for the "different" condition only. b) In Experiment 2, objects were assembled in order to create blocks of no-change (*NC*), shape-change (*SC*), texture-change (*TC*) and color-change (*CC*) stimuli.

In Experiment 1, behavioral data were collected for patients DF and MS, and eight age-matched controls, performing same/different discrimination tasks between pairs of stimuli differing only in either shape, or color, or texture (Figure 1a).

In Experiment 2, twelve neurologically intact participants, along with patient DF and patient MS, took part in a fMRA experiment in which no change (*NC*), shape change (*SC*), texture change (*TC*) and color change (*CC*) blocks of trials (Figure 1b) were intermingled with periods of fixation. To maintain their attention throughout the experimental session, we asked participants to perform a one-back task, by pressing a button with the right index finger whenever an image was immediately repeated. This implies that even within the "change" blocks, a stimulus was sometimes presented twice. The logic of the fMRA technique assumes that neuronal populations within a given cortical region are sensitive to specific aspects of a stimulus. This sensitivity is assessed by measuring the attenuation (reduction) or rebound (increase) of the BOLD signal in response to a pair of stimuli in which the second stimulus has been modified in one dimension only. If the BOLD signal is attenuated then it is inferred that the neuronal population is not sensitive to the changed dimension (because it responds as if the stimulus is repeated identically). If the BOLD signal shows a rebound then it is inferred that the neuronal population *is* sensitive to the changed dimension.

Participants: Experiments 1 and 2

Two brain-damaged patients (DF and MS) participated in both experiments. DF is right-handed and MS is left handed.

Patient DF has a profound visual form agnosia as a consequence of a hypoxic episode which damaged her lateral occipital cortex bilaterally (Milner AD *et al.*, 1991). Structural MRI shows that DF's most clearly-defined lesions overlap well with

the location of area LOC in the ventral stream of healthy subjects, along with a further small focus of damage in the left posterior parietal cortex (James et al., 2003). Along with her failure to recognize objects visually, she has particular difficulties in discriminating shape, lightness, orientation and symmetry. Despite these deficits she has relatively well-preserved visual acuity, color vision, tactile recognition and verbal intelligence.

Patient MS has a left homonymous hemianopia (with macular sparing), along with profound achromatopsia, prosopagnosia and visual object agnosia, as a consequence of a presumed idiopathic herpes encephalitis infection that caused extensive damage to his ventromedial occipito-temporal cortex bilaterally. His left hemisphere damage includes the temporal pole, the parahippocampal and fourth temporal gyri of the temporal lobe, the collateral sulcus and the mesial occipito-temporal junction (the latter damage presumably causes MS's achromatopsia: see Zeki S, 1990). The first, second and third temporal gyri are intact and the frontal and parietal lobes are preserved in their entirety. Lesions within the right hemisphere encompass the same regions damaged in the left, with the addition of the second and third temporal gyri and the striate cortex (producing a left homonymous hemianopia). For a more extensive case description of MS, see (Heywood CA et al., 1994; Newcombe F and Ratcliff G, 1975). Although MS has a profound object agnosia, he does not have visual form agnosia, since he can readily discriminate between different shapes.

Eight age-matched controls (four females; age range 51-60) also participated in Experiment 1, and ten young participants (six female; age range: 22–42) and two older males (age 51 and 60) participated in Experiment 2. All of them were right-handed as measured by the Edinburgh Handedness Inventory (Oldfield RC, 1971), all

had normal or corrected-to-normal vision, and none had any history of neurological disorder. All participants (patients and intact controls) underwent repeated functional scans as well as one anatomical scan during the same session and gave informed consent before beginning the experiment, which was approved by the Ethics Committees of Durham University and York Neuroimaging Centre (YNiC).

Stimuli: Experiment 1 and 2

The virtual 3D stimuli used in the experiment were created using the software package Autodesk Maya Unlimited 2008 (Autodesk, San Rafael, CA). Shapes can be created in this package by stretching a 'skin' over a skeleton defined by a set of lines in 3D space. Objects with random shapes were created by a custom program which built random skeletons constrained to fit within virtual boxes with predefined minimum and maximum sizes. The package also provides texturing options ('Maya Fur') which can be controlled by a wide range of parameters (e.g. texture element density, length, correlation, orientation, curl etc.). A custom program generated objects with random textures by varying these parameters randomly within predefined limits. The pigments of the underlying 'skin' and of all of the texture elements were defined to be identical. Objects with random colors were produced by varying the red, green and blue reflectances of these pigments randomly between predefined limits. One shape, texture and color was chosen as the arbitrary standard object used in the no change (NC) condition. Sets of objects which departed from this standard in terms of one feature only, either shape, texture or color, were created using the procedures outline above (a total of 115 prototypes for each category). The same sets of objects were used in both Experiments 1 and 2. It is worth noting that it is inevitable that the textures covering objects that differ in shape in the *SC* condition will be different

instances of a common type of texture. It would be possible to generate different instances of the same type of texture in the *CC* and *NC* sets. There is, however, no obvious way of applying the same logic to color. As we are particularly concerned with equating change in the *TC* and *CC* sets we therefore chose to retain identical unchanging tokens of texture in the *CC* set and unchanging tokens of color in the *TC* set.

Apparatus and procedures:

Experiment 1

Experimental stimuli were created by arranging images of the objects from the sets described above into pairs vertically aligned on the right side of the screen, centered at an eccentricity of 6.65 degrees of visual angle. The stimuli measured 15 x 6 cm at a viewing distance of 60 cm. Lateralized presentation was chosen to facilitate object discrimination for patient MS, who has a left hemianopia. In half of the trials the pair of objects was identical and in the other half it was different. Same/different judgments were performed within the same visual feature (i.e. between two shapes, two textures or two colors). For both same and different trials, stimuli were not perfectly aligned vertically and were left/right flipped in order to avoid visual discrimination based on symmetry. To reduce cognitive demands caused by frequent task changes, shape, texture and color discriminations were performed in blocks of 30 trials. Participants were informed at the beginning of each block as to the feature they were about to discriminate. In each trial, stimuli were presented for 4 s and subjects were required to perform a discrimination by signalling verbally whether the stimuli were “same” or “different”. Verbal report was chosen over manual report to avoid confounds associated with difficulties the patients might have learning/remembering

the correct stimulus/response associations. Age-matched controls were tested in one session while DF and MS underwent two separate sessions.

Experiment 2

Subjects lay comfortably supine inside the bore of the scanner, with their head fixed in order to minimize movements. Stimuli were back-projected (Dukane 8942 ImagePro 4500 lumens LCD projector) onto a custom in-bore acrylic rear projection screen and were viewed through a mirror mounted on the head coil.

We used a block design experiment where stimuli were organized into *SC*, *TC*, *CC* and *NC* blocks. In each block, a series of stimuli were presented for 800ms each, with a 200ms ISI (blank screen). *SC* blocks consisted of 13 unique objects which differed in their geometric shape, but not in their texture or color. *TC* blocks consisted of 13 unique objects differing in the type of surface texture, but identical in underlying shape and color. *CC* blocks consisted of 13 unique objects which varied in color, but maintained the same texture and shape. In *NC* blocks we presented an identical stimulus (which was different from those used in the other blocks) 14 times. Each block of stimuli was intermingled with a period of fixation (which was used as a baseline condition). Because we asked our participants to perform a one-back task, during *SC*, *TC* and *CC* blocks one of the stimuli, and its location within the block, was randomly repeated.

Each run was organized into a series of 16 blocks of stimuli (4 blocks per condition) and 17 blocks of fixation, each one lasting 14s, for a total duration of 7:42 minutes. During the fixation period a 0.54° x 0.54° black cross was presented on a white background. Each subject performed 4 experimental runs.

Stimuli were presented in the center of the screen and measured 6 x 6 cm at a viewing distance of 60cm. Participants were instructed to look at the fixation point during the baseline period, but to move their eyes freely if they so desired when the experimental stimuli were presented[1]. They were also asked to perform a one-back task by pressing a button with the right index finger. Stimuli were controlled by Presentation software (version 9; Neurobehavioral Systems Inc, Albany, USA). Manual responses were collected via keypads (*Lumitouch* pads – Photon Control, Inc, Burnaby, BC, Canada).

Imaging parameters.

All participants were tested at the York Neuroimaging Centre (UK), using a 3-Tesla whole-body GE *Excite* MRI system. A High Density Brain Arrays 8 channels head coil was used in all experiments. Blood oxygenation level-dependent (BOLD)-based functional MRI volumes were collected using optimized T2*-weighted segmented gradient echo planar imaging (26 cm FOV, with a 64x64 matrix size for an in-plane resolution of 3 mm, RT = 2 s, TE = 30 ms, FA = 90 deg). Each volume was composed of 40 contiguous slices of 3 mm thickness, angled at approximately 30 deg from axial, to sample occipital, parietal, posterior temporal and posterior/superior frontal cortices. During each experimental session, a T1-weighted anatomic reference volume was acquired along the same orientation as the functional images using a 3D acquisition sequence (scan parameters: RT=7.8 ms, TE=3 ms, FA=20 deg, matrix size=256×256, FOV=256×256 mm2, 176 slices, slice thickness=1 mm, no gap, total scan time=5 min 3 s).

[1] Free viewing was allowed to equate the experimental setting for patient M.S. who, having a left hemianopia, needed to move his eyes to see the stimuli entirely. Following the arguments of Cant and Goodale (2007), we believe that the deployment of attentional resources to the geometric *vs* surface features of the object would not grossly affect the viewing strategy applied by participants during the discrimination task.

Data analysis

Behavioral data

In Experiment 1, accuracy scores of the age-matched controls were analyzed using a repeated-measures ANOVA and paired comparison t-tests. Single-subject data for MS and DF were analyzed using binomial and χ^2 tests.

In Experiment 2, accuracy scores of the controls during the *SC*, *TC* and *CC* conditions were analyzed using a repeated-measures ANOVA on the number of correct reports. For DF and MS, accuracy data were gathered but not analyzed, since some of the experimental conditions did not exceed the minimum five values difference required by χ^2 tests.

Imaging data (Experiment 2)

Data were analyzed using *BrainVoyager QX* software (version 1.9; Brain Innovation, Maastricht, Netherlands). For each subject, functional data underwent 3D motion correction algorithms. No deviations larger than 1 mm translations or 1º rotations were observed in the motion correction output. Functional data were then pre-processed with linear trend removal and underwent high-pass temporal frequency filtering to remove frequencies below three cycles per run. Anatomical volumes were transformed into standard stereotaxic space (Talairach J and Tournoux P, 1988). Functional volumes were then aligned to the transformed anatomical volumes, thereby transforming the functional data into a common stereotaxic space across subjects.

The fMRI data were analyzed using a general linear model (GLM), and a random-effect GLM was used for the group average analysis. The model included four experimental predictors (*SC*, *TC*, *CC* and *NC*) and 6 motion correction predictors

(x, y, z for translation and for rotation). The period of fixation (14s) was used as a baseline. The experimental predictors were modelled as a transient (14s) epoch where the square-wave function for each phase was convolved with the default *Brain Voyager QX* "two-gamma" function designed to estimate hemodynamic response properties. Prior to analysis, the data were z-normalized; thus beta weights extracted from the active clusters represent an estimate of the magnitude of activation for each condition (constrained by the shape of the expected HRF) in units of z-scores.

In the averaged voxelwise group analysis, statistical activation maps were set to reliable threshold levels and cluster volumes ($p< 0.001$, minimum cluster size =373 mm^3) using Monte Carlo simulations (performed using *BrainVoyager QX*) to verify that our regions of interest were unlikely to have arisen by chance as a consequence of multiple comparisons.

After identifying the areas that were activated by a comparison of interest using odd runs only (runs 1 and 3), we performed analyses on the beta weights (β) extracted from the even runs only (runs 2 and 4). The use of separate data sets to localize the activated brain areas and to evaluate the different patterns of activity within them circumvents the problem of "circular analysis" (Kriegeskorte N et al., 2009), where the independence of statistical tests for selective analysis (in this case β *values*) is invalidated by the bias present in the comparisons used to select the areas (procedures sometimes called "double dipping"). *Beta* values (β) for even runs only were extracted for each area, each subject and each condition separately and were analyzed using repeated-measures ANOVAs and corrected post hoc comparisons. While Sidak adjustments for multiple comparisons were used for the main effects, two-tailed t-test statistics (corrected for the numbers of planned comparisons) were

used to scrutinize significant interactions. The t-test statistics were computed using subject-related variability as error estimates.

Single-subject imaging data on MS and DF were pre-processed and analyzed as described above. Significant activations were defined in each individual by contrasting conditions (using separate study predictors in order to weight for the contribution of each run) at a threshold of $p<0.001$, uncorrected. Patients MS and DF performed the main fMRI adaptation experiment for less than 4 runs (DF a total of 2 runs and MS a total of 3 runs), therefore separate datasets could not be used for the selection and selectivity analyses, as they were for the control subjects.

Results

Experiment 1

Behavioral results

In a repeated-measures ANOVA on the accuracy of the age-matched controls, TASK (shape vs texture vs color) did not reach significance ($F_{(2,14)}$=2.384, p=0.129), showing that performance did not differ across the three discrimination tasks (shape=87%, texture=90% and color=91%; Figure 2). In contrast, our patients DF and MS obtained performance scores that differed markedly across the three discriminations, and they showed an opposite pattern of results from each other. DF's performance rose above chance only for the texture [74% (53/72), p=0.0001] and color [85% (61/72), p=0.0001] discriminations, which were significantly more accurate [χ^2(1)=5.9, p=0.015 and χ^2(1)=15.8, p=0.0001] than her shape discrimination [54% (39/72)]. DF's scores on texture and color discrimination were not statistically distinguishable [χ^2(1)=2.7, p>0.10]. Conversely, patient MS performed above chance *only* for shape discrimination [81% (58/72), p=0.0001], which was significantly more accurate than his texture [χ^2(1)=12.5, p=0.0001] and color [χ^2(1)=11.4, p=0.001] discrimination [52% (38/72) and 54% (39/72), respectively], which again were not statically distinguishable [χ^2(1)=0.03, p=0.87] from one another. When DF and MS were compared with each other, we found that shape discrimination was significantly better in MS [χ^2(1)=11.4, p=0.001], whereas texture [χ^2(1)=6.7, p=0.01] and color [χ^2(1)=15.8, p=0.0001] discrimination were significantly better in DF.

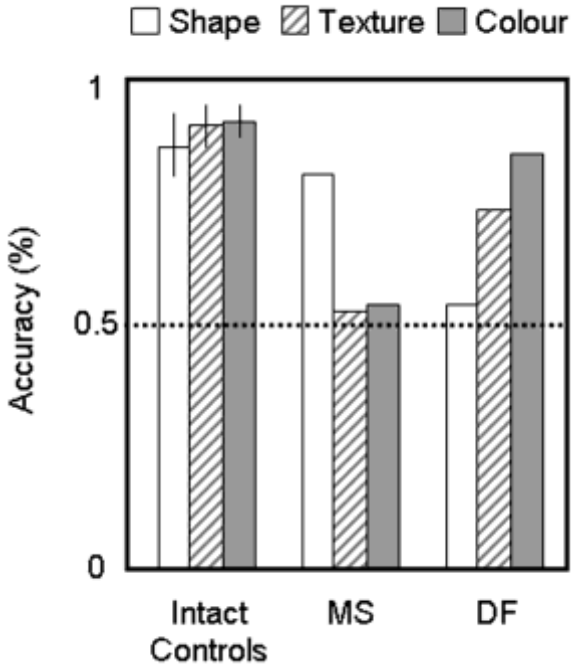

Figure 2. Percent correct responses for shape (white), texture (lined) and color (grey) trials plotted separately for intact age-matched controls, patient DF and patient MS. Bars represent standard errors. The horizontal dotted line represents chance level.

Experiment 2

In order to isolate the neural correlates of shape, texture and color discrimination, we carried out conjunction analysis and standard pair comparisons analysis. Although standard subtraction logic can be usefully applied to experiments involving two conditions that differ in one or more cognitive components, in our paradigm the investigated differences should emerge most clearly by the comparison of multiple experimental conditions. For example, shape selective voxels should rebound only when shape is changed (*SC*), and not when there is no change (during *NC*, *TC* and *CC* blocks). It follows that shape selective voxels should respond more strongly for *SC* as compared with *NC,* for *SC* as compared with *TC* and for *SC* as compared with *CC*. In conjunction analyses multiple paired-comparisons are adjoined

with an 'and' function assuring that only those voxels that significantly satisfy all contrasts simultaneously are selected (Cavina-Pratesi C et al., 2006). As such, they can provide more rigorous evidence with respect to the neural substrates of the presumptive cognitive process than single contrasts alone (Price CJ and Friston KJ, 1997). Just as for shape voxels, we expect texture and color selective voxels to respond only when texture (*TC*) or color (*CC*) is changed as compared with when it is not changed (*NC*, *SC* and *CC* for texture and *NC*, *SC* and *TC* for color).

For all comparisons, we will focus our results and discussion within the occipito-temporal cortices, while reporting stereotaxic coordinates for all active foci in Tables 1 and 2.

Imaging results in neurologically intact participants

Behavioral results for one-back task

In a repeated-measures ANOVA on the accuracy of the neurologically intact participants, TASK (shape vs texture vs color) did not reach significance ($F_{(2,22)}$=0.042, p=0.96). Performance in the scanner was equally accurate across the three discriminations (shape=97%, texture=97% and color=97%).

Separate activations for Shape, Texture and Color processing

Conjunction analysis

Shape processing

To extract voxels selectively responsive to shape, we compared shape change trials with no shape change trials in a conjunction analysis using odd runs only (see Methods) as follows: [(*SC*>*NC*)&(*SC*>*TC*)&(*SC*>*CC*)]. We found bilateral foci of activation along the lateral occipito-temporal cortex and one focus of activation in the

left dorsal extrastriate visual cortex (Table 1). As shown in Figure 3a (highlighted in red) the bilateral activations were congruent with the more dorsolateral portion of the lateral occipital complex (e.g. Malach R et al., 2002), named LO. The more dorsal activation (not shown in the figure) was located at the very posterior end of the left intraparietal sulcus (pIPS) and it may correspond to area V3A (Tootell RBH et al., 1997).

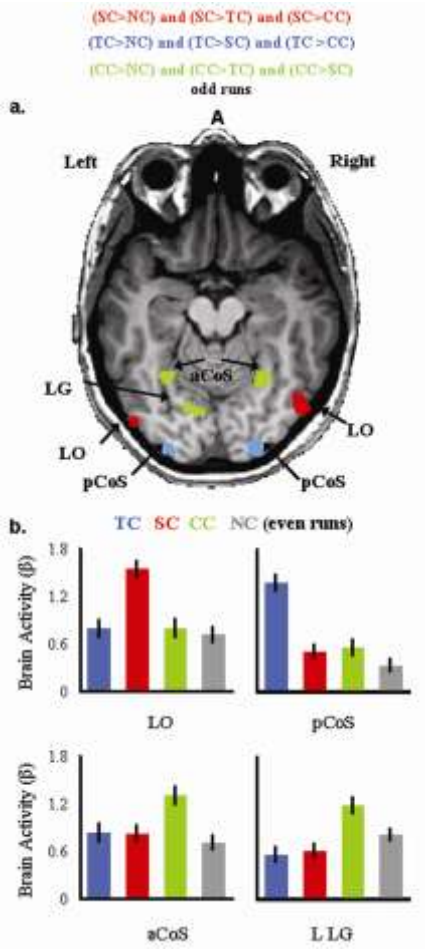

Figure 3. Group activation maps and beta weights for shape, texture and color.

a) Rebound from adaptation for shape change trials [(*SC*>*NC*)&(*SC*>*TC*)&(*SC*>*CC*)] in red, for texture change trials [(*TC*>*NC*)&(*TC*>*SC*)&(*TC*>*CC*)] in blue & for color change trials [(*CC*>*NC*)&(*CC*>*TC*)&(*CC*>*SC*)] in green. *SC* activates bilateral LO.

TC activates bilateral pCoS. *CC* activates bilateral aCoS and left LG. The group activation map is based on the Talairach averaged group results using odd runs only, shown for clarity on a single subject's anatomical scan. b) Averaged beta weights (β) extracted from even runs only measured in each brain area for *SC*, *TC*, *CC* and *NC* blocks. Bars represent standard errors. L=left, R=right, A,a=anterior, p=posterior, LG=lingual gyrus, LO=lateral occipital cortex, CoS= collateral sulcus. *SC*=shape change, *TC*=texture change, *CC*=color change, *NC*=no change.

Table 1: Brain areas active in the contrasts of interest.
LO=Lateral occipital cortex; pIPS=posterior intraparietal sulcus; pCoS=posterior collateral sulcus; aCoS=anterior collateral sulcus; LG=lingual gyrus; FG=fusiform gyrus; DPLC=dorsolateral prefrontal cortex; mIPS= medial intraparietal sulcus; preSMA=pre-supplementary motor area; a=anterior; p=posterior. *SC*=shape change, *TC*=texture change, *CC*=color change, *NC*=no change.

Brain Areas	**Hemisphere**	**Talairach Coordinates**			**Volume mm^3**
		x	*y*	*z*	
Shape Change *[(SC>NC)|&(SC>TC)&(SC>CC)]*					
LO	Left	*-44*	*-75*	*-5*	1501
	Right	*43*	*69*	*-4*	3734
pIPS	Left	*-23*	*-85*	*24*	374
Texture Change *[(TC>NC)&(TC>SC)&(TC>CC)]*					
pCoS	Left	*-23*	*-84*	*-13*	1652
	Right	*16*	*-88*	*-12*	2609
Color Change *[(CC>NC)&(CC>SC)&(CC>TC)]*					
aCoS	Left	*-30*	*-50*	*-13*	376
	Right	*28*	*-50*	*-13*	1082
LG	Left	*-10*	*-76*	*-8*	727
Anterior Insula	Left	*-31*	*20*	*9*	1252
DLPC	Left	*-38*	*1*	*27*	1911
	Right	*32*	*-2*	*32*	565
mIPS	Left	*-29*	*-60*	*39*	730
	Right	*27*	*-48*	*34*	390
preSMA		*-5*	*18*	*47*	753
Shape and Color and Texture *[(SC>NC)&(TC>NC)&(CC>NC)]*					
aFG	Left	*-35*	*-50*	*-14*	492
	Right	*33*	*-44*	*-14*	441
pFG	Left	*-32*	*-73*	*-12*	1217
	Right	*25*	*-73*	*-11*	390

Texture processing

To extract voxels selectively responsive to surface texture, we compared texture change trials with no texture-change trials in a conjunction analysis using odd runs only (see Methods) as follows: [(*TC*>*NC*)&(*TC*>*SC*)&(*TC*>*CC*)]. As reported in Table 1 and Figure 3a (highlighted in light blue), there were bilateral activations lying caudally to the CoS (henceforth referred to as pCoS), in congruence with the location of texture activations reported in previous literature (Cavina-Pratesi C *et al.*, 2009; Peuskens H *et al.*, 2004).

Color processing

To extract voxels selectively responsive for surface color we compared color-change trials with no-color-change trials in a conjunction analysis using odd runs only (see Methods) as follows: [(*CC*>*NC*)&(*CC*>*SC*)&(*CC*>*TC*)]. As shown in Figure 3 (highlighted in green), a bilateral focus of activation was found along the anterior portion of the CoS (henceforth referred to as aCoS) while a single left lateralized focus lay caudally in the lingual gyrus (LG). These activations are congruent with the location of color-selective areas found in the ventral surface of both humans and macaque monkey using fMRI (Wade A et al., 2008). Other active areas were found within the parietal (medial intraparietal sulcus, mIPS) and frontal cortices (anterior insula, dorsolateral prefrontal cortex and pre-supplementary motor area – pre-SMA, see Table 1).

Pattern of Brain activity

Although the pattern of activation between the change and no-change conditions within each localized area is predicted by the specific comparisons we applied, the exact relationship between the no-change conditions (including *NC* proper and the feature-of-no-interest change conditions) remains open. One of the criticisms made of adaptation paradigms is that the conditions where the same stimuli are constantly repeated are less interesting for the participants as compared with the ones in which the stimuli are changing continuously. This might cause the subjects to pay less attention to the same-stimulus conditions as compared with the changing ones. Such an attentional imbalance could of course explain the higher response for *SC*, *TC* and *CC* trials as compared with *NC* trials. In order to test the exact relationship between all experimental conditions within the activated area in the ventral stream, beta weights (β) were extracted for each participant and each activated area using even runs only (see Methods) and were subjected to several ANOVAs. First, given that most of the areas were bilateral we ran a repeated-measures ANOVA using HEMISPHERE (left, right), BRAIN AREA (LO, pCoS, aCoS) and TRIAL TYPE (*SC*, *TC*, *CC, NC*) as factors. Only the main effect of TRIAL TYPE ($F_{(3,33)}$=11.55, p<0.0001) and the interaction of BRAIN AREA x TRIAL TYPE ($F_{(6,66)}$=11.8, p<0.0001) reached significance. Post-hoc paired-comparisons on the main effects showed that β values for *NC* trials were significantly lower (p values ≤ 0.014) than *SC*, *TC* and *CC* trials, which were not statistically distinguishable from each other. However, and more interestingly for our purpose, post-hoc t-tests corrected for the number of comparisons in the interaction (3 areas x 4 tasks → 0.05/12=0.0042) showed that each area exhibited a specific rebound from adaptation for one feature change only, leaving all the other conditions statistically

indistinguishable. More specifically, as shown in Figure 3b, area LO showed significantly higher β for *SC* than for *TC* ($p<0.0001$), *CC* ($p<0.0001$) or *NC* ($p<0.0001$), which did not differ from each other (*p* values ≥ 0.676). Area pCoS showed significantly higher β for *TC* than for *SC* ($p<0.001$), *CC* ($p<0.0001$) or *NC* ($p<0.0001$), which did not differ from each other (p values ≥ 0.185). Lastly, area aCoS showed significantly higher β for *CC* than for TC ($p<0.0001$), *SC* ($p<0.002$) or *NC* ($p<0.004$), which did not differ from each other (p values ≥ 0.263). Given that differences between hemispheres did not reach significance, in a second ANOVA we compared activations for all brain areas (including the unilateral response within LG excluded from the previous analysis) across hemispheres using BRAIN AREAS (LO, pCoS, aCoS, LG) and TRIAL TYPE (*SC*, *TC*, *CC, NC*) as factors. Again we found a significant main effect of TRIAL TYPE ($F_{(3,33)}=3.795$, $p<0.019$) and interaction of BRAIN AREA x TRIAL TYPE ($F_{(9,99)}=14.75$, $p<0.0001$). Planned post-hoc t-test comparisons on the interaction (4 areas x 4 tasks → 0.05/16=0.0031) showed that activations for LO, aCoS and pCoS were identical to the ones reported above. More importantly, color-selective voxels within LG showed the same pattern of activation as aCoS voxels, with a significantly higher β for *CC* than for TC ($p<0.0001$), *SC* ($p<0.003$) or *NC* ($p<0.0001$), which did not differ from each other (p values ≥ 0.209). Overall, the lack of differences between the *NC* and the 'feature-of-no-interest' change conditions in all areas suggest that differences in activation were truly feature-specific and not driven by nonspecific attentional factors.

Separate paired comparisons analysis

It is possible to argue that using conjunction analysis to demonstrate the existence of independent subsystems might have introduced a bias, dictating to some degree the

outcome as "independent" rather than "interactive" processing. We therefore carried out separate analyses using single-pair comparisons and independent localizers, to localize shape, texture and color areas. First, following the logic of (Cavina-Pratesi C *et al.*, 2009) we compared *SC* vs *TC* using odd runs only. We found bilateral foci of activation along the more lateral and dorsal parts of the lateral occipito-temporal cortex (LO, see Figure 6a, supplementary materials, depicted in red). Second, using a similar logic, we compared *TC* vs *SC* using odd runs only, and found bilateral activations lying within the pCoS (Figure 6a, supplementary materials, depicted in blue). For completeness, we also compared SC vs CC and TC vs CC, and again we found bilateral activations within LO and pCoS, respectively (see Figure 6a supplementary material, depicted in orange and light blue, respectively). Given the importance of the comparison between texture and color in the present investigation, brain activity for *pCoS* was extracted from the voxels localized using *TC* vs *CC*. Third, we used an independent color localizer contrasting color vs grayscale paintings (see supplementary materials: independent localizer 1), and found significant activations bilaterally within the aCoS and within the left LG (figure 6a, supplementary materials, depicted in dark green). For completeness, brain activity for color is also reported for the paired comparisons of *CC* vs *TC* (Figure 6a, supplementary materials, depicted in light green) and *CC* vs *SC* (Figure 6a, supplementary materials, depicted in bright green) using odd runs only. Talairach coordinates for all active areas are reported in Table 3, supplementary materials. Brain activity (in terms of β, extracted for the even runs only) was analysed using repeated-measures ANOVAs. Brain activity for color was extracted from the areas localized by the independent comparison of color > grayscale paintings. First, given that most of the areas were bilateral we ran a repeated-measures ANOVA using HEMISPHERE

(left, right), BRAIN AREA (LO, pCoS, aCoS) and TRIAL TYPE (*SC*, *TC*, *CC, NC*) as factors. Only the main effect of TRIAL TYPE ($F_{(3,33)}$=13.34, p<0.0001) and the interaction of BRAIN AREA x TRIAL TYPE ($F_{(6,66)}$=10.42, p<0.0001) reached significance. Corrected post-hoc paired-comparisons on the main effects showed that β values for *NC* trials were significantly lower (*p* values ≤ 0.028) than *SC*, *TC* and *CC* trials, which were not statistically distinguishable from each other. However, and more interestingly for our purpose, post-hoc t-tests corrected for the number of comparisons in the interaction (3 areas x 4 tasks → 0.05/12=0.0042) showed that each area exhibited a specific rebound from adaptation for one feature change only, leaving all the other conditions statistically indistinguishable. More specifically, as shown in Figure 3b, area LO showed significantly higher β for *SC* than for *TC* (p<0.0001), *CC* (p<0.0001) or *NC* (p<0.0001), which did not differ from each other (*p* values ≥ 0.736). Area pCoS showed significantly higher β for *TC* than for *SC* (p<0.0034), *CC* (p<0.001) or *NC* (p<0.002), which did not differ from each other (*p* values ≥ 0.526). Lastly, area aCoS showed significantly higher β for *CC* than for TC (p<0.001), *SC* (p<0.0001) or *NC* (p<0.001), which did not differ from each other (*p* values ≥ 0.131). For the conjunction analysis, given that no differences between hemispheres reached significance, we compared activations for all brain areas (including the unilateral response within LG excluded from the previous analysis) across hemispheres, in a second ANOVA using BRAIN AREAS (LO, pCoS, aCoS, LG) and TRIAL TYPE (*SC*, *TC*, *CC, NC*) as factors. Again we found a significant main effect of TRIAL TYPE ($F_{(3,33)}$=8.90, p<0.0001), and interaction of BRAIN AREA x TRIAL TYPE ($F_{(9,99)}$=19.08, p<0.0001). Planned post-hoc t-test comparisons on the interaction (4 areas x 4 tasks → 0.05/16=0.0031) showed that activations for LO, aCoS and pCoS were identical to those ones reported above. Most importantly, color-selective voxels

within LG showed the same pattern of activation as aCoS voxels, with a significantly higher β for *CC* than for TC ($p<0.0025$), *SC* ($p<0.0001$) or *NC* ($p<0.0022$), which did not differ from each other (p values ≥ 0.099).

Common activations for shape, texture, and color

Conjunction analyses can also be used to identify brain areas that are jointly activated by shape, texture and color together. It is possible that some neurons might be driven by a conjunction of features, and would therefore record a rebound from adaptation for all types of feature change, relative to *NC*. The logic is identical to the one applied above: if one voxel is selective for shape, texture and color, then it should significantly rebound from adaptation for *SC* versus *NC*, for *TC* versus *NC*, and for *CC* versus *NC*. We performed a conjunction analysis using even runs only (see Methods) [(*TC*>*NC*)&(*SC*>*NC*)&(*CC*>*NC*)] and activations were found bilaterally along the fusiform gyrus (FG), both anteriorly (aFG) and posteriorly (pFG, Table 1 and Figure 4 – highlighted in yellow). β values from these areas (depicted in Figure 4b) were subjected to a repeated-measures ANOVA using HEMISPHERE (left, right), BRAIN LOCATION (anterior, posterior) and TRIAL TYPE (*SC*, *TC*, *CC, NC*) as factors. All the main effects reached significance, showing lower levels of activation in the left hemisphere ($F_{(1,11)}=6.25$, $p<0.029$), in the more anterior portion of FG ($F_{(1,11)}=31.43$, $p<0.0001$) and for the *NC* blocks ($F_{(3,33)}=20.56$, $p<0.0001$) as compared with all the others (*SC*, *TC*, *CC; p* values ≤ 0.001), which were not statistically distinguishable from each other (p values = 1.0).

Although activations along the FG could arguably be driven by the higher attentional resources devoted to the more difficult one-back task performed on the change blocks as compared to the no-change blocks, we do not consider this to be

likely. If the common activated areas along the bilateral FG were indeed driven by attention, then it is not clear why the fronto-parietal "attentional network" (Corbetta M et al., 2008; Corbetta M and Shulman GL, 2002) was not active as well (no frontal or parietal areas were active for the conjunction analysis of [(TC>NC)&(SC>NC)&(CC>NC) in Table 1]). It is unlikely that top down attentional effects due to task load would activate voxels in visual areas but not in parietal and frontal cortices. We hypothesize instead that the activations along the FG reflect the activity of neurons that are truly responsive to the three features jointly, perhaps neurons receiving information from geometric and surface areas that are selective for higher-level stimuli such as faces and places. Figure 4a shows that activations along the FG partially overlapped with some of the voxels selectively responsive for faces versus places in the fusiform face area (FFA, anterior pink dotted lines, Figure 4a) and for places versus faces in the posterior lingual gyrus (pLG, posterior brown dotted lines, Figure 4a), mapped by the use of an independent localizer (see supplementary material: independent localizer 2). The locations of these areas agrees well with those previously reported for some of the foci associated with face and place stimuli (Epstein RA et al., 2007; Kanwisher N et al., 1997). To verify that the overlap was truly driven by the conjunction of shape, texture and color, we extracted brain activity (β) for *SC*, *TC*, *CC* and *NC* from the voxels that were activated by both the face and place independent localizers and by the conjunction analysis of [(*TC>NC*)&(*SC>NC*)&(*CC>NC*)]. Brain activity extracted from the voxels in which the conjunction analysis overlapped with left FFA (14 voxels), right FFA (64 voxels), left pLG (180 voxels), and right pLG (275 voxels), were then subjected to a repeated-measures ANOVA using HEMISPHERE (left, right), BRAIN LOCATION (FFA, pLG) and TRIAL TYPE (*SC*, *TC*, *CC, NC*) as factors. Only the main effects of

HEMISPHERE ($F_{(1,11)}$=66.2, p<0.0001) and TRIAL TYPE ($F_{(3,33)}$=27.3, p<0.0001) reached significance, showing lower activity within the left hemisphere, and more importantly, for the *NC* as compared to all the change tasks (all p values < 0.0001). In addition *SC*, *TC* and *CC* were mutually indistinguishable (all p values ≥ 0.45).

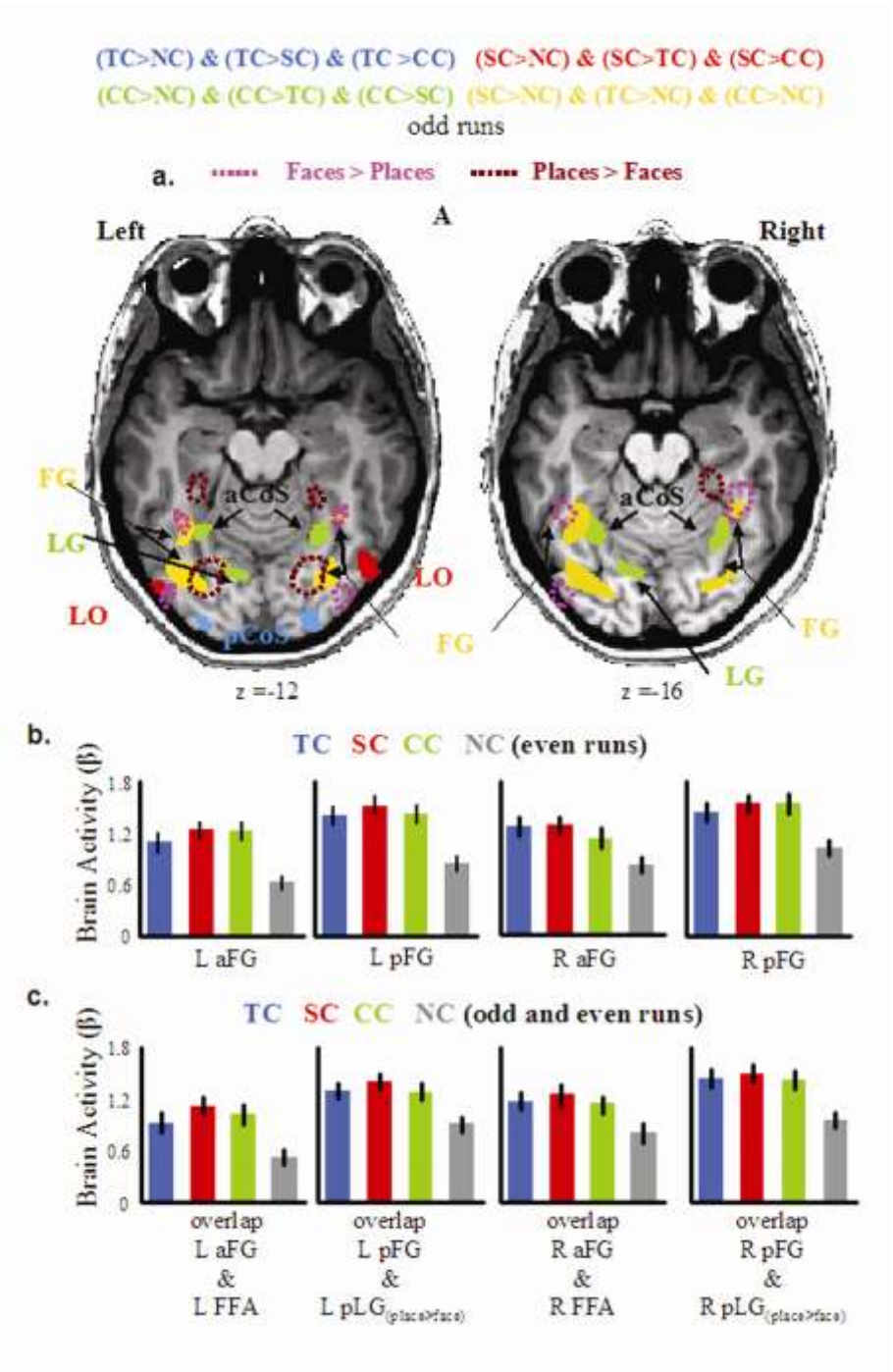

Figure 4. Group activation maps and beta weights for selective and common areas. a) Rebound from adaptation for shape change trials [(*SC*>*NC*)&(*SC*>*TC*)&(*SC*>*CC*)] in red, for texture change trials [(*TC*>*NC*)&(*TC*>*SC*)&(*TC*>*CC*)] in blue, for color change trials [(*CC*>*NC*)&(*CC*>*TC*)&(*CC*>*SC*)] in green and for the common activation of shape, texture and color trials [(*SC*>*NC*)&(*TC*>*NC*)&(*CC*>*NC*)] in yellow. Activations for faces versus places (pink dotted lines) and places versus faces (dark brown dotted lines) from separate localizer runs are also reported. Common activations for *SC*, *TC* and *CC* are localized bilaterally along the anterior and medial portion of the FG. As before, the group activation map is based on the Talairach averaged group results using odd runs only, shown for clarity on a single subject's anatomical scan. b) Averaged beta weights (β) extracted for even runs only measured in the common brain areas for *SC*, *TC*, *CC* and *NC* blocks. c) Averaged beta weights (β) extracted for even runs only from the voxels in which the common activated brain areas overlapped with the brain areas active for face versus place (left and right FFA) and for place versus face (left and right pLG). Bars represent standard error. FG=fusiform gyrus; other abbreviations as in Figure 3.

<u>*Common activations for texture and color*</u>

In order to test for the existence of brain areas jointly activated by texture and color but not by shape, we performed a conjunction analysis using odd runs only as follows: [(*TC*>*NC*)&(C*C*>*NC*)&(*CC*>*SC*)&(TC>SC)]. No significant active voxels were found at the selected threshold.

Imaging results for patients DF and MS

Behavioral results for one-back task

DF's and MS's accuracy in the scanner was similar to those recorded for the behavioral task. DF performed better for texture (6/8 correct; 75%) and color (6/8 correct; 75%) than for shape (4/8 correct; 50%). MS showed the opposite trend: he could discriminate between shapes (9/12 correct; 75%) but not between textures (5/12 correct; 41%) or colors (6/12 correct; 50%).

Separate activations for Shape, Texture and Color processing

Conjunction analysis

Shape processing

Overlaid activation maps for shape change trials as compared with no-shape-change trials using a conjunction analysis [(*SC*>*NC*)&(*SC*>*TC*)&(*SC*>*CC*)] are shown in Figure 5 (highlighted in red). We focused our single-subject analyses around area LOC, given its well-known role in form perception (Grill-Spector K et al., 2001) and our results on neurologically intact participants. Talairach coordinates for all brain areas active for the above comparison in the two patients are reported in Table 2.

Patient MS showed one focus of activation within the left lateral occipital cortex (Figure 5c) and one focus of activation within the dorsal bank of the calcarine sulcus (calcD). Talairach coordinates overlapped well with the dorsal subdivision of LOC, namely the lateral occipital area (LO). The level of brain activity (β), reported here for completeness but not analysed quantitatively, was higher for *SC* than for *NC*, *TC* or *CC,* indicating a clear preference for the geometry of the stimuli (Figure 5d). No activation was found in the right hemisphere. MS's activation in terms of both location and β is similar to the results found in the left hemisphere of the control participants (see single subjects' activations in supplementary material, Figure 7).

Patient DF showed no activation within LOC or its subdivision LO. This result is consistent with the fact that her lesion (yellow arrows in Figure 5a) overlaps greatly with the locus of activation seen in control participants and patient MS.

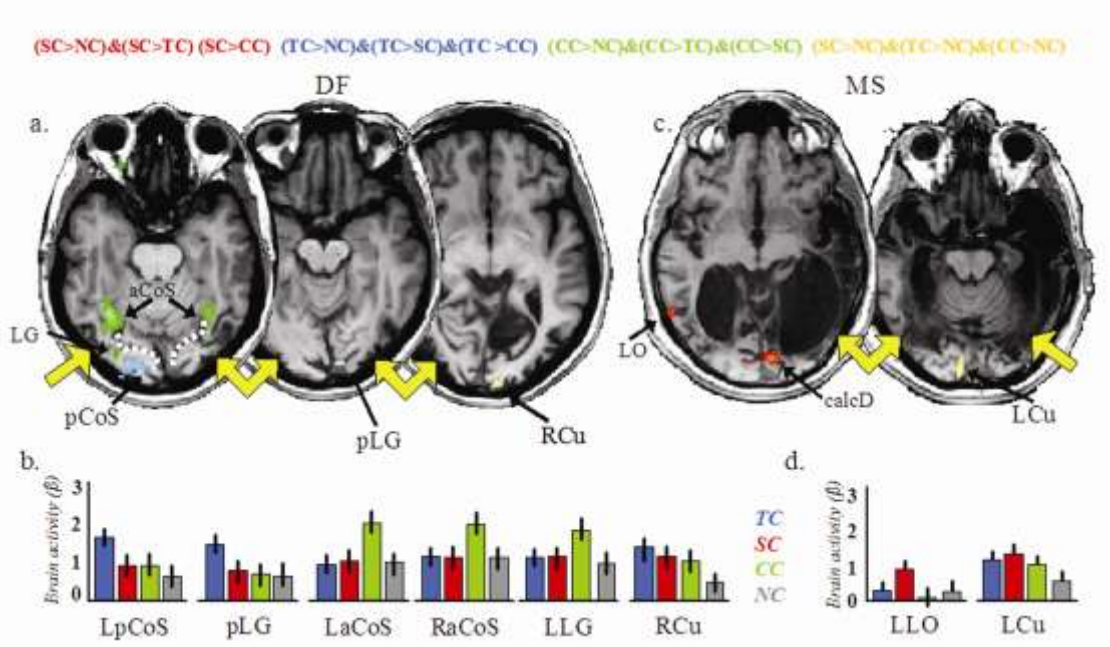

Figure 5. Activation maps and beta weights for shape, texture and color in patients. Rebound from adaptation for shape change trials [(*SC*>*NC*)&(*SC*>*TC*)&(*SC*>*CC*)] in red, for texture change trials [(*TC*>*NC*)&(*TC*>*SC*)&(*TC*>*CC*)] in blue, for color change trials [(*CC*>*NC*)&(*CC*>*TC*)&(*CC*>*SC*)] in green and for the common activation of shape, texture and color trials [(*SC*>*NC*)&(*TC*>*NC*)&(*CC*>*NC*)] in yellow. *SC* activates left LO in patient MS only (c). *TC* activates right pCoS and left pLG in patient DF only (a). Color change activates bilateral aCoS and left LG in DF only (a). Common activations for *SC*, *TC* and *CC* are localized within LCu in MS (c) and RCu in DF (a). b,d) Averaged beta weights (β) measured in each brain area for *SC*, *TC*, *CC* and *NC* blocks. Yellow arrows highlight principal brain lesions. calcD=dorsal calcarine; Cu=cuneus; other abbreviations as in Figure 3.

Table 2: Brain areas active for the contrasts of interest in patients MS and DF. LO=lateral occipital area; calcD=dorsal calcarine; Cu=cuneus. Other abbreviations as in Table 1.

Brain Areas	Hemisphere	Talairach Coordinates			t value
		x	y	z	
Shape Change *[(SC>NC)&(SC>TC)&(SC>CC)]*					
Patient MS					
LO	Left	*-58*	*-56*	*-4*	3
calcD	Right	*5*	*-80*	*7*	3
mIPS	Left	*-30*	*-60*	*53*	3
	Right	*26*	*-67*	*48*	3
Patient DF		n.a.			
Texture Change *[(TC>NC)&(TC>SC)&(TC>CC)]*					
Patient DF					
pCoS	Left	*-16*	*-87*	*-20*	3
pLG	Right	*21*	*-91*	*-5*	3
Patient MS		n.a.			
Color Change *[(CC>NC)&(CC>SC)&(CC>TC)]*					
Patient DF					
aCoS	Left	*-32*	*-60*	*-20*	3
	Right	*33*	*-52*	*-20*	3
LG	Left	*-30*	*-74*	*-23*	3
Anterior Insula	Left	*-30*	*15*	*10*	3
DLPC	Left	*-43*	*23*	*30*	3
	Right	*45*	*27*	*25*	3
mIPS	Left	*-43*	*-51*	*32*	3
	Right	*39*	*-52*	*30*	3
preSMA		*-2*	*8*	*47*	3
Patient MS		n.a.			
Shape & Color & Texture *[(SC>NC)&(TC>NC)&(CC>NC)]*					
Patient MS					
Cu	Left	*-4*	*-83*	*-14*	3
Patient DF					
Cu	Right	*8*	*-92*	*-9*	3

Texture processing

Overlaid activation maps for texture change trials using a conjunction analysis [(*TC>NC*)&(*TC>SC*)&(*TC>CC*)] are shown in Figure 5 (highlighted in blue).

Patient DF showed two foci of activation: one was located at the posterior end of the left CoS (Figure 5a) and the second was found in the right posterior lingual

gyrus (pLG). The level of brain activity (*β)* for the activated area in pCoS, reported here for completeness but not analysed quantitatively, was higher for *TC* than for *NC*, *SC* or *CC*, which showed comparable overall responses (Figure 5b). DF's activation pattern in terms of both location and β is similar to the results found in control participants (see single-subject activations in the supplementary material, Figure 7).

Patient MS showed no activation within the occipital lobe. This result is consistent with the fact that his lesion encompasses all of the medial aspect of the occipital lobe (yellow arrow, Figure 5d), including the active foci found in control participants and in patient DF.

Color processing

Overlaid activation maps for color change trials using a conjunction analysis [(*CC>NC*)&(*CC>SC*)&(*CC>TC*)] are shown in Figure 5 (highlighted in green). As before, we focused on the temporo-occipital cortex, but stereotaxic coordinates for all active areas are reported in Table 2.

Patient DF showed bilateral activations within the aCoS and one focus of activation slightly caudally within the left LG (Figure 5a). *Beta* values, again reported for completeness but not analysed quantitatively, was higher for *CC* than for *NC*, *SC* or *TC* (which showed comparable overall responses) in all three areas (Figure 5b). DF's activations in terms of both location and β are similar to the results found in the control participants (see single-subject activations in supplementary material, Figure 7).

Patient MS showed no activation for color (Figure 5c). As before, this result is consistent with the fact that his lesion encompasses all of the medial aspect of the

occipital lobe, including all the active foci found in control participants and in patient DF

Separate paired-comparisons analysis

Just as for the controls, we localized shape, texture and color areas using single paired comparisons and independent localizers. First, we compared *SC* vs *TC* and *SC vs CC,* and found for both contrasts a left lateralized activation along the more lateral and dorsal portion of the lateral occipito-temporal cortex in patient MS only (LO, see Figure 8a, supplementary materials, depicted in red and orange respectively). Second, we compared *TC* vs *SC* and *TC vs CC,* and found for both contrasts a left lateralized activation lying within the pCoS of patient DF only (see Figure 8a, supplementary materials, depicted in light blue and dark blue, respectively). Third, we used an independent color localizer contrasting color vs grayscale paintings (see supplementary materials), and found significant activations bilaterally within the aCoS and within the left LG, in patient DF only (see Figure 8a, supplementary materials, depicted in dark green). The level of activity (β) for left LO and pCoS and aCoS bilaterally (reported for completeness but not analyzed quantitatively) reflected the pattern of activity found previously in the conjunction analysis. For completeness, we have also reported brain activity for the paired comparison of *CC* vs *TC* (Figure 8a, supplementary materials, depicted in light green). Talairach coordinates for all active areas are reported in Table 4, supplementary materials.

Common activations for Shape, Texture and Color processing

Just as for the neurological intact participants, we ran conjunction analyses to isolate areas that are jointly activated by shape, texture and color, using

[(*TC*>*NC*)&(*SC*>*NC*)&(*CC*>*NC*)]. Unilateral activations were found only within the right cuneus (Cu) of patient DF and the left Cu of patient MS, perhaps in correspondence with early visual areas. Activation maps, β values and Talairach coordinates are shown in Figure 5 (highlighted in yellow) and Table 2.

Common activations for texture and color

As for the intact control participants, we performed a conjunction analysis using [(*TC*>*NC*)&(C*C*>*NC*)&(*CC*>*SC*)&(TC>SC)] to test for the existence of brain areas activated by surface features in general. No significant active voxels were found at our chosen threshold.

Discussion

In the present study we confirmed previous evidence of the role played by lateral and medial occipito-temporal cortices in discriminating geometric (shape) and surface (color and texture) features, respectively (Experiments 1 and 2). More importantly, we found that the medial occipito-temporal cortex contains separate foci for processing different surface features of a given object. In particular, while color-related activity was localized anteriorly within the CoS and the LG, texture-related activity lay more caudally within the CoS (Experiment 2). We also showed that areas *selective* for shape, texture and color were quite distinct from those areas that respond to all of these features (shape and texture and color) *together.* The latter were found to correspond closely with some of those associated with the perception of more complex stimuli such as faces and places. Finally, we tested two patients with object recognition difficulties following different patterns of ventral-stream damage. We showed that a disruption or sparing of the surface-feature selective areas, *versus* a

reciprocal sparing or disruption of area LO, was associated with a loss of discrimination for the corresponding feature/s (texture or color *versus* shape) along with successful discrimination on the other/s (Experiments 1 and 2).

Shape

A selective rebound from adaptation for object shape was found in an area identifiable with LO. This area is part of the so called 'object area' (LOC) which has been traditionally localized by contrasting images of intact objects versus scrambled versions of the same images (Malach R et al., 1995). Recent findings have refined the function of this area, which is now associated specifically with the extraction of shape *per se,* rather than with either the specific contours comprising the shape (Kourtzi Z and Kanwisher N, 2000; Vinberg J and Grill-Spector K, 2008), or the visual cue (texture, motion, color or luminance) used to define the shape (Georgieva SS et al., 2008; Grill-Spector K et al., 1998; Self MW and Zeki S, 2005). This definition fits perfectly with the idea that the LO subdivision of LOC responds more vigorously when asked to deal with the geometric rather than the surface properties of objects in the present and previous (Cant JS *et al.*, 2009) adaptation experiments.

Texture

A selective rebound from adaptation for texture was localized more medially, within the pCoS bilaterally. These foci fit with previous reports of texture (Cavina-Pratesi C *et al.*, 2009) and surface-pattern related (but not strictly texture-related) activations (Peuskens H *et al.*, 2004). However, unlike previous studies (Cant JS *et al.*, 2009; Cant JS and Goodale MA, 2007; Peuskens H *et al.*, 2004) we did not find activations within the lingual sulcus/gyrus nor in the anterior collateral sulcus. This may be

because unlike the stimuli used in those previous studies, our texture stimuli did not include color variation (being constructed as purely grayscale images), and their texture was defined solely through local small-scale variations of the structure of their surfaces. Unlike the stimuli used in those previous studies, our textural stimuli *only* varied in the micro-geometry of their surfaces (not to be confused with the macro-geometry of their overall shape). In other words, they differed in texture defined as a 3D property that could be detected by touch as well as by vision (Ho YX et al., 2008; Koenderink JJ et al., 2007). We would draw a distinction between *texture* as a micro-geometric property of surfaces, and *pattern* as a property in which coloration varies in some recognizable fashion over the surface of an object. A zebra, for example, has a more or less uniform horse-hair *texture* but a *pattern* of irregular black and white stripes. Some of the objects used in previous studies varied in both pattern and texture in our terms, which may account for the differences between the activations we found and those reported in those earlier studies. One might reasonably have concern about this result in pCoS if the stimuli in the *TC* blocks differed from the other blocks in terms of low-level visual properties such as spatial frequency content. One might intuit that the *TC* would vary more than the others in terms of contrast and therefore it would activate the pCoS more given its location near retinotopic cortices. To address this issue we computed the power spectra across spatial frequencies for the luminance component of all of our images. We then computed the coefficient of variation (the standard deviation of power divided by the mean) at all frequencies for each stimulus type as the coefficient of variation should best predict the extent of adaptation to variation in low-level properties of the stimuli. It turned out that the shape stimuli (*SC* block) produced higher average power than *CC* and *TC*. Importantly, the coefficient of variation is remarkably similar across nearly all frequencies for *TC* and *SC*. At the

lowest frequencies the coefficient of variation for *TC* and *CC* are similar (a graph of the coefficients of variation is presented in the supplementary Figure 10). This pattern of variability rules out the possibility that *TC* adaptation in pCoS is attributable to a confounding effect of contrast activating retinotopic areas.

Color

A selective rebound from adaptation for surface color was found medially within the left LG and the aCoS (bilaterally). These locations fit well with color-related areas V4/V8 (Hadjikhani N *et al.*, 1998; McKeefry DJ and Zeki S, 1997) or VO1 (Brewer AA et al., 2005) and V4α (Bartels A and Zeki S, 2000) or the anterior color area (Murphey DK et al., 2008), respectively.

Previous studies have failed to isolate brain areas truly selective for color as opposed to texture. Common activations for all combinations of color, texture and shape have been reported within several ventral areas, mostly within anterior and medial portions of the FG (Cant JS *et al.*, 2009; Cant JS and Goodale MA, 2007). Not surprisingly, these locations are very similar to the joint activations that we found for *TC*, *SC* and *CC* in the present study. The absence of specific activations in known color areas in Cant and co-workers' results might be related both to the nature of their visual stimuli and the task demands they used. As we noted above, they used stimuli with complex surface features varying in both texture and pattern resembling real materials such as laminated oak, metallic paint, marble and tinfoil, whereas our texture stimuli simply varied in surface micro-geometry. Their stimuli may also have differed more than ours in other surface properties such as reflectance and specularity. As a consequence of these differences, it is possible that the processing areas localized by Cant and co-workers were responsive to combinations of features

(including color), rather than to individual surface features *per se*. For example, behavioral studies have clearly shown that the surface feature of glossiness can be represented in conjunction with other surface features such as coarser scales of 3D texture (Ho YX *et al.*, 2008).

Another factor that might have facilitated the identification of color areas in our study is the task. Whereas Cant and Goodale (2009) used a passive viewing paradigm, we asked our participants to perform a one-back task and therefore to pay attention to each stimulus feature. Attentional modulation has been widely found within color areas (Maunsell JH and Treue S, 2006), and may have contributed to the activations we observed.

Common neural activations during shape, color and texture discrimination

Brain areas showing single-feature selectivity for shape, color or texture sit beside other areas that respond to all of the features together. These multi-feature areas lie within the FG, extending toward both the anterior and the posterior portions of the gyrus. Neurons selective for multiple features of objects have been reported in the inferior temporal (IT) cortex of macaque monkey. While some neurons respond to either shape and color (Komatsu H et al., 1992), others are modulated by different combinations of shapes, colors and patterns (Komatsu H and Ideura Y, 1993). IT neurons have been found to show either selective responses to three-dimensional texture or to a combination of these same textures and shapes (Koteles K et al., 2008). It should be noted however that within a single voxel there are thousands of neurons and therefore it is not possible for us to trace back our conjunction activations to either neurons selective to all features simultaneously or to overlapping populations of neurons each singly selective for color, texture and shape. Areas of common

activation for shape, color and texture along the FG overlap quite well with voxels selective for more complex visual stimuli such as scenes (pLG, Epstein RA *et al.*, 2007) and faces (FFA, Kanwisher N *et al.*, 1997). Cant and Goodale (2007) similarly found a compelling overlap between areas selective for material properties and areas selective for places and faces. Presumably the identification of such complex stimuli relies on combinations of features including shape, color and texture. Indeed, current models of scene recognition postulate the use of surface cues such as color (Oliva A and Schyns PG, 1997) and texture (Renninger LW and Malik J, 2004) in the rapid categorization of scenes (scene "gist"). Similarly, when asked to discriminate faces, observers do not use only shape (local/global, Liu J et al., 2009; Schiltz C and Rossion B, 2006), but rely also on surface features such as skin color and pigmentation (Bruce V and Langton S, 1994; Nestor A and Tarr MJ, 2008; Vuong QC et al., 2005).

Causal roles of lateral and medial occipito-temporal cortices in geometric and surface feature processing

If the fMRI activations within lateral and medial occipito-temporal cortices truly reflect a division of labor for the extraction of surface and geometric features of objects respectively, then DF's spared medial occipito-temporal areas might underlie her ability to use color and texture to help recognize objects (Humphrey GK *et al.*, 1994). Similarly, MS's spared right lateral occipital cortex might account for his intact ability to distinguish shapes. Our behavioral results in Experiment 1 confirmed a double dissociation between patients DF and MS. While DF showed above-chance texture and color discrimination but no significant shape discrimination, MS showed the converse pattern, performing above chance only for shape discrimination. In

parallel with this behavioral double dissociation, Experiment 2 showed that DF's lesion included the region where brain activity was higher for shape than texture and color in our control subjects and in patient MS while, conversely, MS's lesion included the region where brain activity was higher for texture and color in the controls and in patient DF. In other words, the brain areas active for shape discrimination in control participants and in MS were compromised in DF's brain and, conversely, the brain areas active for texture and color discrimination in control participants and in DF were compromised in MS's brain. This pattern of results argues for specific *causal* roles of LO in shape discrimination and pCoS and aCoS in the discrimination of surface features such as texture and color. The necessary participation of LO in object discrimination confirms previous work (Cavina-Pratesi C *et al.*, 2009; Ellison A and Cowey A, 2006; James TW et al., 2003). The novelty of our results lies in the fact that we have narrowed the causal role of LO to overall macro-geometry, specifically excluding the surface indentations or colors of objects. Similarly, perceptual impairments have been previously reported in the neuropsychological literature for both texture (Battelli L et al., 1997; Cavina-Pratesi C *et al.*, 2009; Vaina LM, 1987), and color (Bouvier SE and Engel SA, 2006), though the extent of their independence from shape discrimination impairments has remained unclear. The present data confirm clearly that the discrimination of surface features is carried out by systems quite separate from those underlying shape discrimination.

Of course our brain lesion data alone do not allow us to argue also for mutually independent mechanisms for texture and color discrimination, since both types of discrimination are spared in DF, and both are impaired in MS. Nevertheless our fMRI data lead us to predict that patients with sufficiently selective lesions to medial occipitotemporal cortex might present a "triple dissociation" between shape,

texture and color deficits. Unfortunately transcranial magnetic stimulation, currently the only viable tool to create virtual lesions in the human brain, cannot reach such medial parts of occipitotemporal cortex, so that the testing of patients with selective brain lesions remains the only method available to assess the causal role played by posterior and anterior portions of the collateral sulcus.

MS's lesion includes the anterior portion of the CoS and the lingual gyrus, near to the well-known color areas V4/V8 (VO1), and V4α (anterior color area) which have been associated with achromatopsia (Heywood CA and Kentridge RW, 2003) since the late seventies (Poppel E et al., 1978). Although our data clearly show that areas in the anterior portion of the CoS and the lingual gyrus are necessary to discriminate colors, it is not yet clear whether these areas are involved in color vision *only* (Bouvier SE and Engel SA, 2006). MS's lesion is extensive and his deficit also includes hemianopia and prosopagnosia, the latter according well with the lack of activity within face-selective areas in his data presented here in Figure 9 of the supplementary material (OFA and FFA). As also depicted in Figure 9, however, DF does show active voxels within FFA, though activation is completely missing more posteriorly in OFA (see also Steeves JKE et al., in press). Separate clusters of voxels selective for faces within FFA/OFA, and for color in aCoS/LG in control participants confirms previous studies (Clark VP et al., 1995), and suggest that the common association of achromatopsia and prosopagnosia might be because the CoS and the fusiform gyrus share the same vascular substrate.

The lack of common activity for *SC*, *TC* and *CC* in patients MS and DF suggests that these areas might play a fundamental role in combining multiple stimulus characteristics to achieve a fully unified representation of particular objects and scenes. Although these common areas of activity along the FG seem to be spared

in DF, they would presumably not receive the full range of stimulus information needed for a unified multidimensional representation.

Surface features

Our data demonstrate for the first time that a brain area selective for texture is located more caudally than the areas selective for color, and that they both lie within the medial portion of the occipito-temporal cortex. This clear functional separation within the medial portion of the ventral stream suggests that individual surface features of objects are processed separately. This is confirmed by behavioral evidence showing not only that form is processed independently from surface properties, but also that surface texture is processed independently from surface color (Cant JS et al., 2008). Likewise, patients have been described in the literature with texture discrimination impairments despite a sparing of color vision (Vaina LM, 1990). It is likely that yet other surface properties of objects are processed within the medial occipitotemporal cortex; one example being a specific brain area responsive for light-emitting as compared with light-reflecting objects within the lingual gyrus (Leonards U et al., 2005). This area might be associated with the perception of glossiness which has been identified as a critical feature in guiding our oculomotor behavior while exploring paintings (Leonards U et al., 2007).

We have found no evidence for any single visual area that identifies surface properties in general, and we suggest instead that a constellation of foci independently extract the different surface features needed for inferring the material that constitutes a given object.

Conclusion and future directions

The existence of separate and common brain foci associated with the perception of objects in terms of shape, color and texture, enriches the realm of possibilities with which we can describe the functional organization of the ventral visual stream. So far visual information has been mapped onto the cerebral cortex depending on its exact location in the visual field (retinotopic mapping) or on the stimulus category it belongs to (objects, faces, places, bodies, words). Our work brings further evidence for an intermediate level of visual mapping, based on the type of visual feature that is being processed. This further level of analysis sits midway between the low and high level processing represented by retinotopic and stimulus category mapping, respectively. Studies directly investigating the relationships between these three different levels of visual mapping, within a single experiment and with the same subjects, will be needed to clarify their respective roles in constructing complete representations of the visual world in the ventral visual cortex.

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